Parental provisioning drives brain size in birds

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Abstract

Larger brains should be adaptive because they support numerous eco- and socio-cognitive benefits, but these benefits explain only a modest part of the interspecific variation in brain size. Notably underexplored are the high energetic costs of developing brains, and thus the possible role of parental provisioning in the evolution of adult brain size. We explore this idea in birds, which show considerable variation in both socio-ecological traits and the energy transfer from parents to offspring. Comparative analyses of 1,176 bird species show that the combination of adult body mass, mode of development at hatching, relative egg mass, and the time spent provisioning the young in combination strongly predict relative brain size across species. Adding adult eco- and socio-cognitive predictors only marginally adds explanatory value. We therefore conclude that parental provisioning enabled bird species to evolve into skill-intensive niches, reducing interspecific competition and consequently promoting survival prospects and population stability. Critically, parental provisioning also explains why precocial bird species have smaller brains than altricial ones. Finally, these results suggest that the cognitive adaptations that provide the behavioral flexibility to improve reproductive success and survival are intrinsically linked to successful parental provisioning. Our findings also suggest that the traditionally assessed cognitive abilities may not predict relative brain size.

Significance statement

Species vary substantially in their brain size, and the idea that larger-brained species are those with a complex social life or enhanced technological skills has generated much interest. Here we explore another explanation. Because the cognitive benefits provided by brains materialize after a long delay, and constructing them independently involves a major bootstrapping problem for the young, parental inputs may be critical for a species' brain size. Comparative analyses of a large sample of bird species show that parental provisioning strongly predicts relative brain size across species, swamping the effects of previously considered social or technological cognitive abilities. Thus, cognitive adaptations in birds that enable successful parental provisioning also provide the behavioral flexibility to improve survival and reproductive success.

Introduction

Brain size varies extensively within and across lineages, and has increased considerably over evolutionary time (1). This intriguing variability has raised questions about the adaptive benefits of increased relative brain size (i.e., relative to adult body mass). An obvious benefit is improved cognitive abilities (2-4), and numerous comparative studies explored this idea. In mammals, work has prominently focused on the social brain hypothesis, which emphasizes the social benefits of relatively larger brains, but eco-cognitive benefits have also been explored (5-7). In birds, work focused on both social drivers, especially pair bond maintenance (5, 7, 8), and ecological ones, especially environmental variability (9-12). Whereas comparative studies have difficulty assessing whether larger brains improve reproductive success, they can more easily show whether they improve survival. Indeed, comparative studies support a positive association between relative brain size and longevity in diverse lineages (13-15).

Other research independently focused on the high energy costs of brain tissue (16, 17). This aspect is pivotal for the expensive tissue hypothesis, which focuses on the trade-off between brain size and other energetically expensive tissues, such as guts (18). Subsequent work highlighted a general link between relative brain size and the energy available to sustaining the brain (19). These costs imply that natural selection cannot always respond to opportunities to evolve specific cognitive adaptations via an increase in brain size, even if this would in principle lead to higher fitness. Indeed, recent comparative work has found that species living in fluctuating environments that cause inevitable reductions of energy intake show reduced relative brain size (20, 21). These trade-offs also have a developmental aspect: the maternal energy hypothesis (22) argues that the ability of mammalian mothers to transfer energy to their offspring constrains brain size (23). Various studies reported a link between maternal allocation and relative brain size in mammals (23, 24), birds (8), cichlid fish (25), and sharks and rays (26). However, they failed to provide an adaptive explanation for this association or did not evaluate alternative or complementary hypotheses.

Here we propose that paying systematic attention to the developmental costs of brains should improve our understanding of brain size evolution via its correlated evolution with

parental provisioning. Offspring face a seemingly insurmountable bootstrapping problem posed by growing and differentiating large brains. How can offspring develop large brains when they would need them to provide the energy necessary for this process? This catch-22 leads to the prediction that adult brain size across species depends on the parents' capacity to provision their young. Thus, we examine the effect of parental provisioning on relative brain size in birds, while simultaneously assessing hypotheses proposing eco- or socio-cognitive benefits. This lineage is well suited for an integrated test of these different hypotheses: birds show appreciable variation in many relevant traits, and the energy transfer from parents to offspring can readily be assessed via egg volumes and the time offspring are provisioned. Moreover, birds have a deeply rooted split in the developmental state of the hatchlings, ranging from precocial (no or little provisioning of the young) to altricial (extended provisioning), henceforth referred to as developmental mode (27). Previous work noted that precocial species have smaller adult brain size than altricial ones (28, 29), but the evolutionary causes of this pattern remain unclear. Birds also vary in the number of providers (30). These differences allow us to distinguish the effects of investment in eggs from those of provisioning of young. Moreover, birds show major variation in ecology (aspects of their ecological niche, the climate in their geographic range) (31) and in sociality (32).

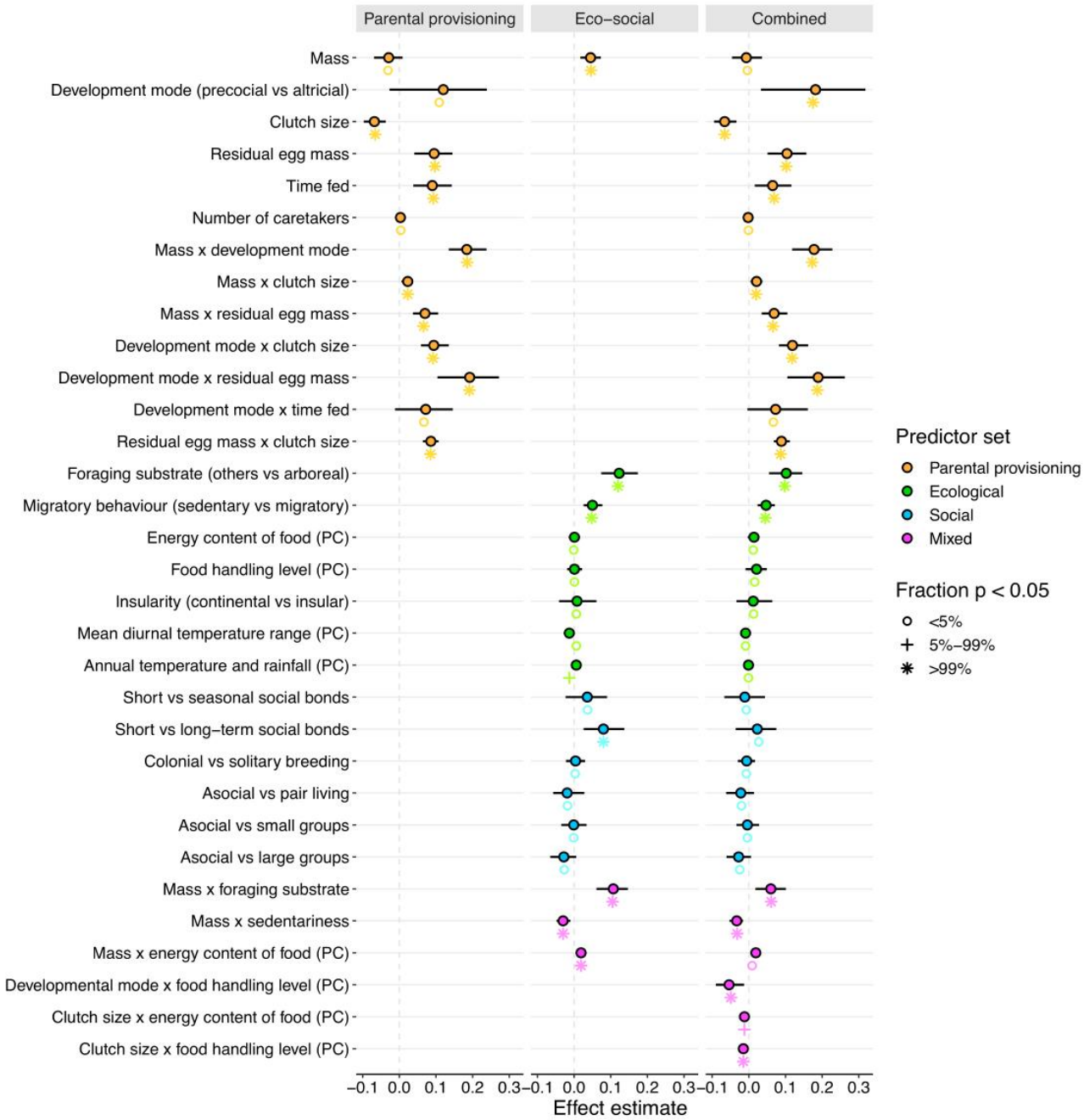
This high variability in all relevant variables in birds allowed us to simultaneously test all these effects on adult brain size. We assembled information on adult brain size, adult body mass, predictors assessing parental provisioning (egg mass, clutch size, duration of food provisioning, number of providers), ecology (fiber and energy content of food, complexity of food acquisition, foraging substrate, sedentariness, insularity, climate in the geographic range), and sociality (strength and stability of pair bonds, breeding alone or in colonies, group sizes outside the breeding season) for 1,176 bird species. For the comparative tests, we used phylogenetically controlled Bayesian mixed models (33) to assess the effects on relative brain size across species of i) parental provisioning, ii) eco-social predictors, and iii) all predictors combined. Next, to understand how the different predictors may have affected each other's evolution, we used phylogenetic d-separation path analysis (34).

Results

Because body mass is tightly correlated with brain size, any model that incorporates body mass as an independent predictor of brain size will tend to mask the impact of the other, more informative predictors. We therefore report the results using relative brain size scaled by body mass as the response variable, but note that analyses including absolute brain size as a response variable produce qualitatively the same results (see S1a-c Table). Moreover, body mass scales many aspects of bird physiology and life-history in a non-linear manner. Thus, we include body mass and its interaction with key predictors in all models to capture these nonlinearities.

Phylogenetically controlled mixed models showed that larger relative brain sizes in birds were positively associated with all components of parental provisioning (Fig 1, S2a-d Tables). Larger relative brains were found in species that are altricial, have larger relative egg mass, smaller clutches, and feed their young for a longer time. The effect of these predictors was modified by interactions among them, further highlighting the importance of parental provisioning (Fig 1). Accordingly, only precocial species showed a negative correlation between relative brain size and clutch size (Fig 2a), while only altricial species showed a positive correlation between relative brain size and the time offspring are fed (Fig 2b). The remaining interaction effects reflected fundamental allometries or differences in body mass between precocial and altricial species (Fig 1). In sum, the total amount of energy invested into each individual young strongly affected adult brain size.

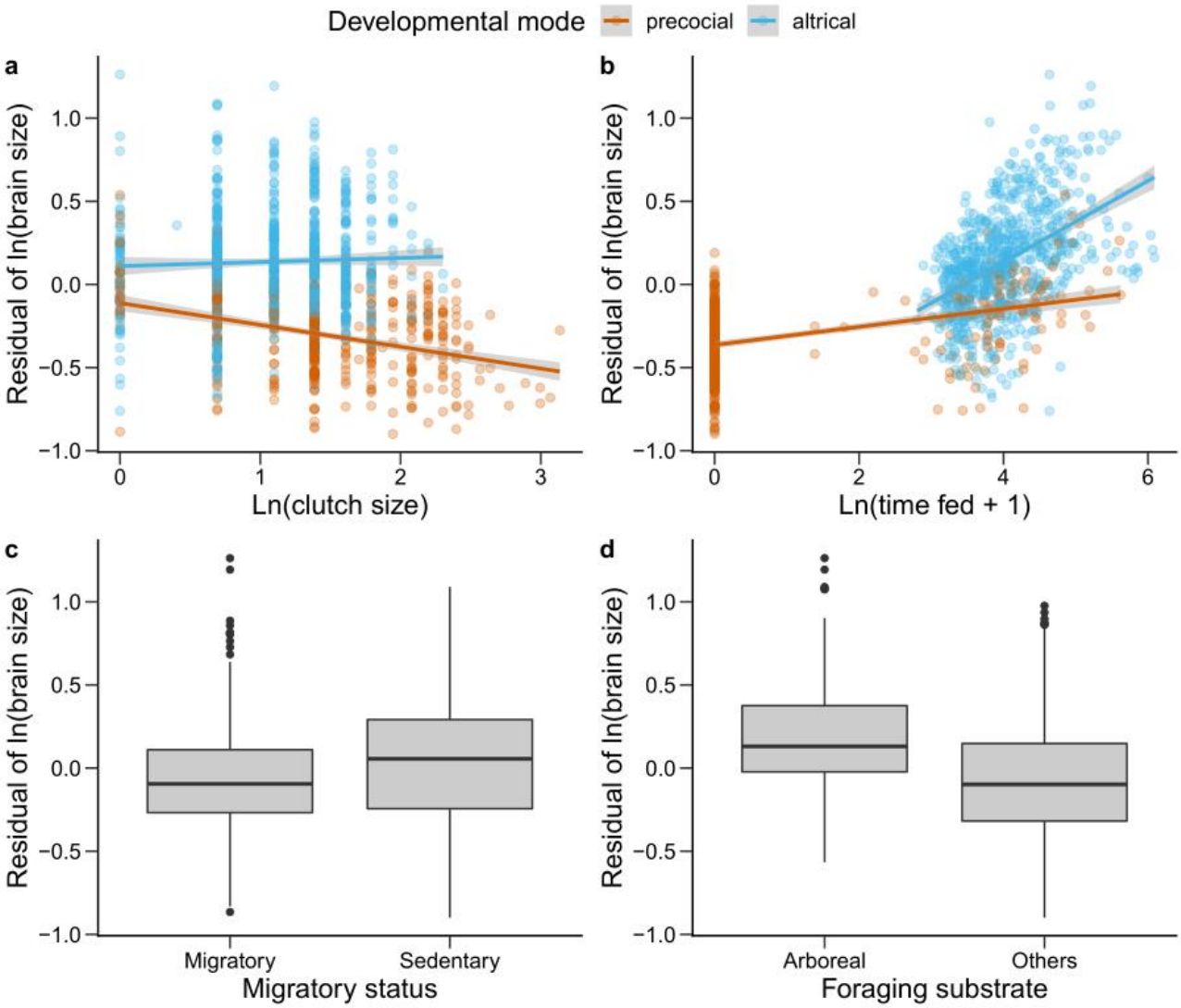
Fig 1. Estimated coefficients and effect sizes of phylogenetically controlled mixed models of the parental provisioning model, the eco-social model, and the combined model on relative brain size in birds. Color-filled circles denote estimated effects, lines denote the 95% lower and upper confidence limits generated in the R package MCMCglmm (33) based on a consensus phylogeny. Symbols below the circles denote the proportion of random tree models that reach statistical significance ($p<0.05$) for each predictor based on model averaging of 200 models, using a set of random trees from http://birdtree.org (35). The corresponding full models are shown in S2a-c Table.



When only examining the effect of eco-social predictors on relative brain size, phylogenetically controlled mixed models primarily showed that sedentary species and those that forage arboreally, had larger relative brain size than those that are migratory or use other foraging substrates (Fig 2c,d). In terms of interaction effects, we found that relative brain size increases with body mass only in arboreal foragers, and that higher energy content of food translated into larger relative brain size only in larger species (Fig 1). Social factors had a much weaker impact on relative brain size: species with enduring pair

bonds tended to have a larger relative brain size than species without pair bonds, whereas no correlations were found for the other social predictors (Fig 1).

Fig 2. The effect of parental provisioning (a, b) and ecological parameters (c, d) on relative brain size in birds (N=1,176 species). a) Clutch size vs developmental mode (precocial vs altricial). **b)** Time provisioned vs developmental mode (precocial vs altricial). **c)** Movement pattern: sedentary vs migratory. **d)** Foraging substrate: others vs arboreal. In **a-b**, solid lines designate linear trend estimates, grey shading designate standard error bands. In **c-d**, thick lines designate medians, the grey boxes designate inter-quantile ranges (IQR, 0.25-0.75 quantile), whiskers designate ±1.5 IQR, circles designate outliers.



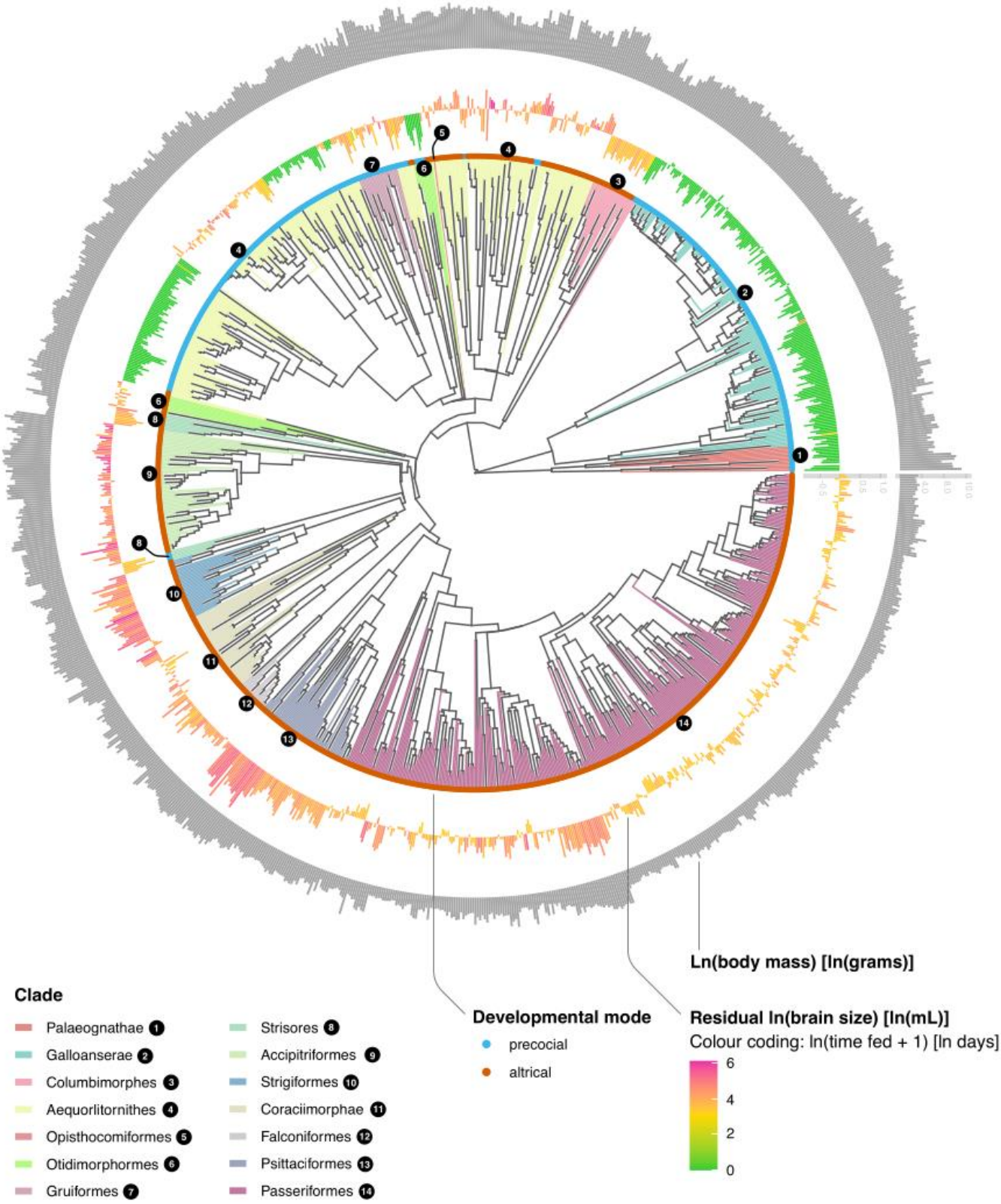
The eco-social model explained markedly less variance in relative brain sizes than the parental provisioning model (R^2 = 0.38 vs R^2 = 0.50). However, a combined model containing both parental provisioning and eco-social predictors performed best (R^2 = 0.57). Although confirming the patterns of the separate models (Fig 1), it revealed that the posterior estimates of effect sizes of parental provisioning were far larger than those of the eco-social factors. Among the latter, the ecological predictors that remain significant in the combined model were largely linked to the adult foraging niche and movement patterns, whereas social predictors no longer played any role.

Additional models showed that data limitations are not responsible for the observed patterns. Models that excluded parameters with limited data availability (time fed, social grouping; S3 a-b Tables) confirmed a key role of parental provisioning for relative brain size. Similarly, using a more detailed categorization of the development mode spectrum instead of binary categorization recovered the same patterns (S3c Table), and so did a model that controlled for the possible confounding effect of longevity on parental provisioning parameters (S2d Table).

The effect of parental provisioning on relative brain size became obvious when superimposed on a phylogenetic tree (Fig 3). Starting at 3 o'clock and moving counter-clockwise, early emerging, precocial lineages had relatively small brains, while inter-dispersed altricial lineages (seabirds, pigeons, hummingbirds, swifts) had slightly larger brains. With the origin of Inopinaves (core land birds) (36) some 65 million years ago, systematic altriciality and extensive parental provisioning arose, resulting in several clusters of notably large-brained lineages, including owls, parrots, and corvids, while one lineage (nightjars) reverted to precociality and small brains. The most recently evolved and highly diverse other passerines were small-bodied and did not have brains of exceptionally large relative size, although they are still relatively larger than those of precocial lineages.

Fig 3. Phylogenetic distribution of relative brain size, developmental mode (precocial vs altricial), and time parent(s) feed their offspring (N=1,176 bird species). Size of bars in outer circle represent body mass (ln(grams)); size of bars in middle circle represents relative brain size (ln(mL)) while their color represents the time parents feed their offspring (ln(days

+ 1)); inner circle represents developmental mode (precocial, altricial). Phylogeny follows birdrtree.org (35), whereas taxonomy largely follows Prum et al. (36), explaining why some clades appear polyphyletic.



207 Because the predictors analyzed above may not only have affected relative brain size directly, but may also have selected for evolutionary changes in values of other predictors and thus affected brain size indirectly, we performed phylogenetic path analyses (34, 37) to
210 gain better insights into the causal relationships between traits. We included well-established developmental and eco-social relationships in all models, but also added biologically plausible ones involving brain size that were varied across the different models.
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The model assessing the relationships among the various parental provisioning predictors of relative brain size showed that adult body mass affects all other traits, including
216 developmental mode (Fig 4a). Both a large adult body mass and altriciality had a negative effect on clutch size and residual egg mass. Altriciality had a strong positive effect on the time offspring are fed, and subsequently on brain size. These patterns reflect established
219 life-history trade-offs and their cascading effects on the total amount of energy transferred from parents to their offspring at the different developmental stages. The remaining effect of body mass on relative brain size depended on developmental mode, reflecting that larger
222 altricial species had larger relative brain sizes than precocial species, relative to what would be predicted from body size alone (see Fig 1). This pattern therefore fully supports the pervasive effect of parental provisioning on a species' brain size.
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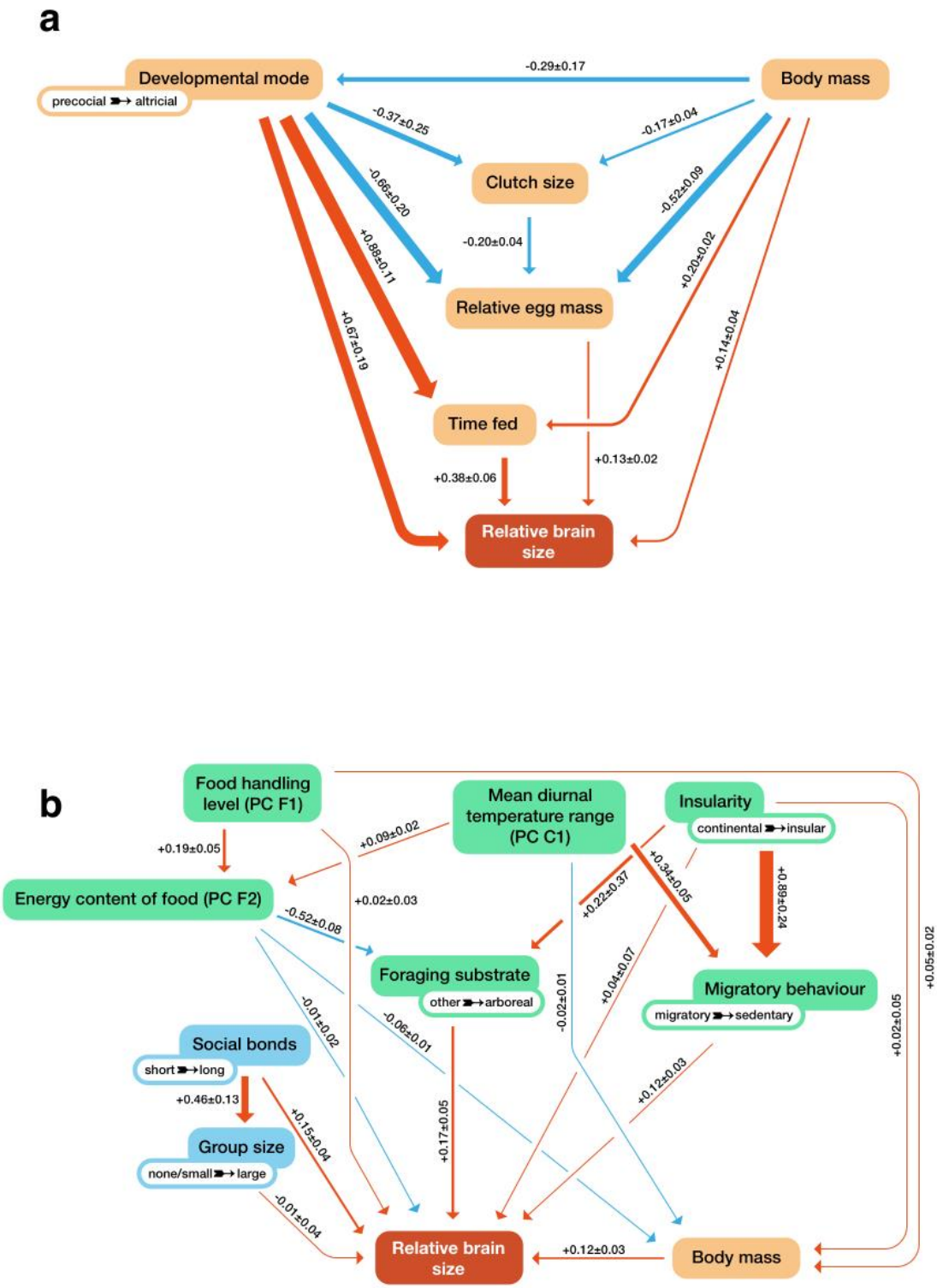
Turning to the eco-social predictors, the path model assessing the evolutionary relationships among them showed that some of these predictors have strong evolutionary links among
228 themselves, but rather weak selective effects on relative brain size (Fig 4b). A combined path analysis (S1 Fig) including both parental provisioning and eco-social predictors retained the relationships revealed by the separate and combined phylogenetically controlled mixed
231 models. Parental provisioning continued to have a direct and strong effect on relative brain size, whereas that of the eco-social variables remains weak.

234 **Fig 4. Phylogenetic associations among predictors and relative brain size, assessed by d-separation path analyses** (34) **(N=1,176 bird species).** Arrows thickness and numeric values show the strength of the association, arrow color shows its direction (positive: orange,
237 negative: blue). **a**, Associations among parental provisioning predictors. **b**, Associations

among eco-social predictors. The plot showing the model including both the parental provisioning and eco-social parameters is shown in S1 Fig.



Discussion

These findings have three major implications, which we now discuss in turn. First, parental provisioning is the main predictor of adult relative brain size in birds: in the combined model, adult eco- and socio-cognitive demands hardly play a role. Thus, large brains can only be sustained in species with extensive energy inputs during development. This association is supported by previous work in diverse lineages (8, 24-26). However, these studies either did not provide an underlying mechanism or did not consider the relationship to reflect adaptation (23, 24). The parental provisioning hypothesis offers a novel theoretical underpinning to this pattern. Parental provisioning enables growing young to construct a large brain during a life stage when they themselves have not yet learned the skills needed to acquire the energy necessary to sustain such a growing and learning brain. Accordingly, parental provisioning removed this bottleneck for the evolution of larger brain size, and enabled bird species to evolve into skill-intensive niches, which reduce interspecific competition and thereby promoting survival prospects and population stability (see (12)). Its importance is also highlighted by the phylogenetic path analyses, which confirm that its components form a tightly coevolved set.

Second, the parental provisioning hypothesis can explain the well-established pattern that altricial species have relatively larger brains than precocial (28, 29). Precocial young are only provisioned through egg mass, which is subject to obvious physical limitations. As a result, they experience serious constraints on relative brain size and therefore niche complexity. The evolutionary transitions to altriciality allowed species to evolve into cognitively more demanding niches, which require more elaborate food-handling or anti-predator skills (29). This was made possible by parents donating the requisite large brain through extended parental provisioning. However, these transitions were actually quite rare (29). Although the underlying reasons for this rarity remain unclear, we speculate that precocial species remain stuck in a simple ecological niche unless they find a way to breed in safer places, which opens the path to provisioning and therefore altriciality.

Finally, our findings imply a modest role at best for socio- and eco-cognitive abilities in the evolution of brain size in birds. We found almost no detectable effect of the cognitive demands of adult social life. We did, however, find weak evidence for effects of eco-cognitive parameters independent of parental provisioning that affect the energy balance of

adults. First, migratory species have smaller brains than resident species (38), indicating that the high energy cost of migration reduces the ability to sustain a large adult brain. Second, the effect of arboreal foraging may be more related to adult survival, as in mammals (39), thus removing a constraint on brain enlargement.

The absence of an effect of the traditionally measured socio- and eco-cognitive variables on relative brain size is puzzling. It may actually reflect a more general problem in comparative cognition, as popular tests often fail to produce a differentiation between species generally thought to show major differences (40). Thus, these tests may not assess those cognitive adaptations that produce fitness benefits by scaffolding critical foraging and predation-avoidance skills and improving the ability to provision the young and/or improve survival. Thus, our results suggest we should pay closer attention to cognitive adaptations such as general behavioral flexibility (as enabled by executive functions and domain-general intelligence (41)), including the coordination of parental duties (essentially linked to planning, decision-making, and time management). These cognitive abilities may be expressed behaviorally in avoidance of predation on eggs, nestlings and adults (42, 43), in maximization of food intake under everchanging food and weather conditions, or in the socio-cognitive ability to coordinate offspring provisioning (5). For example, some birds flexibly adjust parenting in response to predation risk to themselves and their nestlings (44), as confirmed experimentally (45). However, because these cognitive abilities are not readily estimated in a way that can be compared across species, they are so far not included in comparative analyses of brain size evolution.

To conclude, the amount and duration of parental provisioning is the key to understand brain size evolution in birds. It could also explain the major differences in relative brain size between endotherms and ectotherms (1), which is broadly correlated with the amount of parental provisioning. Moreover, it may also apply to human evolution because we humans have the largest relative brain size among all animals, and parents and other caregivers engage in provisioning children well into adolescence (46).

Methods

Data collection

We gathered information quantifying parental provisioning and the socio-ecological correlates identified by previous work as influencing brain size in animals. We collected these data from the online version of the Handbooks of the Birds of the World (47), region specific handbooks (48, 49), existing published datasets (32, 50-52), as well as species specific studies listed in the dataset. Data on brain size were collected from three sources (9, 10, 53).

The following parental provisioning predictors were included: adult body mass, developmental mode, egg mass, clutch size, the time offspring are fed by their parents until nutritional independence, and the number of caretakers. We did not use imputed data based on mean values of related species, which limited our sample size compared to other comparative studies. Adult body mass data were calculated as means if mass of males and females were listed separately. The developmental mode was assessed dichotomously. Precocial species are those which hatch with open eyes and abandon the nest within 2 days after hatching, and here also encompass semi-precocial species (young hatch with open eyes and are soon capable of walking, but they remain in the nest to be fed by parents). Altricial species are those in which young hatch with closed eyes and largely lack feathers and are fed by parents in the nest, and here also encompass semi-altricial species (young hatch with open eyes and are feathered, but remain in the nest to be fed by their parents) (29). Given that this dichotomous split could obscure patterns, we did re-run the main analyses using all four categories (fully precocial, semi-precocial, semi-altricial, fully altricial). Egg mass was either assessed through direct measurements of egg mass, or was calculated based on egg measurements, using the formula by Hoyt (54). For those species where multiple egg dimension measurements were available in the literature, the mean values of all provided measurements were used. For those species where egg dimension or mass data were not available in handbooks, we used information in published data compilations listed in the dataset (52, 55-57). Clutch size data corresponded to the median clutch size (43, 57). The time young are fed by their parents included both the time parents provision their young in the nest as well as thereafter until young are nutritionally independent from their parents, as reported in handbooks (see above), and published datasets (28). We also included the mean number of caretakers, where mound-nesting species had zero caretakers, species with uniparental care one, species with bi-parental care two, and

cooperatively breeding species the mean value of caretakers. These data were obtained from handbooks (47), existing datasets (30, 53), and species-specific studies listed in the dataset.

Based on previous studies on the drivers of brain size in vertebrates, the following ecological predictors were included: food energy, fiber content of food, number of processing steps required to extract food, foraging substrate, sedentariness, insularity, and climatic predictors. The predictors relating to food were calculated based on an existing database (50). We calculated the mean energy and fiber content of foods per 100g from previous studies (19, 58), as well as the number of processing steps required to extract food (59). Given that these three predictors are highly correlated (that is, low caloric food usually has a high fiber content and requires only a single processing step), we used a PCA approach and extracted two independent PCs from these predictors (see below). The foraging substrate data were obtained from a published database (51). We categorized species into those that forage arboreally, compared to all other foraging substrates. In mammals, arboreal foraging has been shown to be associated with increased longevity, which in turn allows the evolution of larger brains (39). Sedentariness was assessed based on the maximum movement pattern of a species, separating sedentary species (including local movements) from migratory species (short- and long-distance migrants, altitudinal migrants), combining data from three sources (9, 32, 51). In addition, we also included data on the insularity of species, distinguishing continental from insular species (11, 51). Missing data were directly obtained from the primary sources listed above. Finally, we included data on the climate in the species' geographic range (60, 61), using a PCA approach (see below). Values of species with contradicting values in different published datasets were confirmed based on the literature listed above, using the above definitions.

The social predictors were also based on previous studies and included social bond strength, group size, and coloniality. Social bond data were based on published data (62), separating species with short bonds during mating only, seasonal bonds, and long-term bonds that extend beyond a single breeding season. The grouping patterns of species outside the breeding season distinguished between asocial species (usually on their own), pair living species (usually in pairs), species that live in small groups (usually 3-30 individuals), and

large groups (usually more than 30 individuals). The split between small and large groups should capture the difference between personalized groups where group members know each other individually, including family groups (32), and ephemeral and/or anonymous groups. We also included whether species breed singly or whether they breed in colonies.

Analyses

All statistical analyses were carried out in the R 4.0.2 environment (63). The analyses were structured as a series of linear models with increasing complexity, all including phylogenetic relatedness across species (in the form of a phylogenetic correlation matrix based on well-resolved avian phylogenetic trees (35)). For predictors that are expected to be allometrically linked to body mass (brain size, egg mass), the models included their residuals from regressions against body mass. Brain size (the response variable) and adult body mass were log-transformed prior to extracting relative brain sizes. All continuous predictors were mean-centered and scaled to a standard deviation of one, to aid in the interpretation of intercepts and the comparison of effect sizes. The three predictors relating to food (food energy, fiber content, food handling levels) were strongly collinear (S4a Table). Thus, we used a Principal Component analysis in the package psych (64) (using varimax rotation) to reduce these predictors to two uncorrelated components. Based on their loadings, the resulting two components describe the energy content of food and the food handling levels (including the absence of fibers) (S4b Table). Using the same approach, we extracted three uncorrelated components from 14 climatic parameters. PC1 reflects a latitudinal gradient from the tropics to high latitudes. PC2 reflects inter-annual variability. PC3 reflects a gradient from dry, open and highly seasonal environments to stable and closed environments.

We fitted three phylogenetically controlled mixed models that assessed the dependence of relative brain size on provisioning predictors (model 1), eco-social predictors (model 2), and a combination of both (model 3). Each model included a set of main effects and first-order interactions with meaningful biological interpretation (see S1-3 Tables for a full list of predictors and interactions in each of the models). Since the size of models (both in terms of data and numbers of predictors) prevented a full search of all predictor combinations via selection based on information criteria (IC), we conducted backward simplification of

models, removing non-significant interactions (starting with the ones having the largest
405 prediction error). To remain conservative, we did not remove non-significant main effects. Backward selection has been shown to perform well in comparison to IC-based model selection in similar contexts (65), and is robust in cases where the number of individual
408 observations exceeds several fold the number of estimated predictors, as is the case here. We report final outputs of the most parsimonious models (Fig 1, S1-3 Tables). All models were fitted using an MCMC-based mixed modelling approach using the package
411 MCMCglmm (33). We used chains of 50'000 iterations, with the first 10'000 iterations discarded as burn-ins and thinned every 40 iterations. Inspection of the final MCMC samples did not show any sign of autocorrelation. All effective sample sizes were close to the actual
414 numbers of sampled draws from predictors' posteriors. In all models, inverse-gamma priors were used for residual variances (parametrized as inverse-Wishart with $V = 1$ and $\nu = 0.002$). The prior for phylogenetic effect was formed as a weakly informative half-Cauchy density
417 (parameter expanded priors with $V = 1$, $\nu = 1$, $\alpha_\mu = 0$ and $\alpha_V = 10'000$). Priors for fixed effects were left as default (Gaussian densities with $\mu = 0$ and large variance). Using a modification of the variance inflation factor (VIF) analysis adjusted to the phylogenetic comparative
420 mixed model used, we verified that none of the other predictors were significantly collinear, as all VIF values were <2 (S5 Table).

423 The necessity of complete information on all predictors reduced the sample size of the main models to 1,176 species. Thus, we fitted additional models excluding those predictors that most strongly limited our sample size: excluding duration of parental provisioning (N=1,458
426 species); excluding duration of parental provisioning and social grouping (N=1,594 species). Both models recaptured the patterns observed in the full model (S2 Table), confirming that our sample was not biased by limited data (S3a-b Tables).
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Subsequent to the phylogenetically controlled mixed models, we conducted phylogenetic path analyses to assess the causal links among the predictors included in parental
432 provisioning, the eco-social and the combined model. Briefly, for each model we defined a set of d-separation statements (34, 37, 66), describing a hypothesis represented by a directed acyclic graph, linking all involved predictors with causal links. We included well-
435 established developmental and eco-social patterns in all models, but also added biologically

plausible relationships that were varied across the different models. The sequence of models considered reflects hypotheses related to brain size predictors, as outlined in S2-4 Figs. The statements were then represented as sets of linear mixed models and fitted using a phylogenetic comparative framework implemented in the ASReml-R package (67). In models involving binary responses (e.g., precocial/altricial), we used generalized linear mixed models with probit link function to fit models, which makes their regression coefficients directly comparable with standardized regression coefficients from general linear models for continuous predictors. Since all continuous predictors were scaled to unit standard deviation, results for categorical predictors can be interpreted as standardized Cohen's d effect sizes, and thus, can be directly compared with continuous standardized regression coefficients. The best-fitting hypothesis in each model set was determined via comparisons of CICc (corrected Fisher's C Information Criterion, a path analysis analogue of AICc (37)). In the parental provisioning and eco-social model, the best model was clearly supported over the alternatives (ΔCICc > 2 for top models). In the combined model, two models were clearly supported over the alternatives, but were conceptually identical (S6 Table).

Code availability

Code used for the analyses and plotting the figures are available from S.M.D. upon request.

Data availability

The data are provided in a supplement.

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Acknowledgements

We thank all field biologists who collected all the natural history data underlying this study. We thank Uri Roll for sharing climatic data.

Funding

M.G.: Heisenberg Grant nr. GR 4650/2-1 by the German Research Foundation DFG.

S.M.D: Polish National Science Centre, grant no. UMO-2015/18/E/NZ8/00505 and Australian Research Council, DECRA award no. DE180100202.

C.P.S: University of Zurich.

Author contributions

M.G. contributed to acquisition of funding, conceptualizing, data collection, data analyses, interpretation of the data, drafting the manuscript.

S.M.D. contributed the data analyses, interpretation of the data.

S.M.G. contributed to data collection, data analyses, revising the manuscript.

C.P. S. contributed to acquisition of funding, conceptualizing, interpretation of the data, drafting the manuscript.

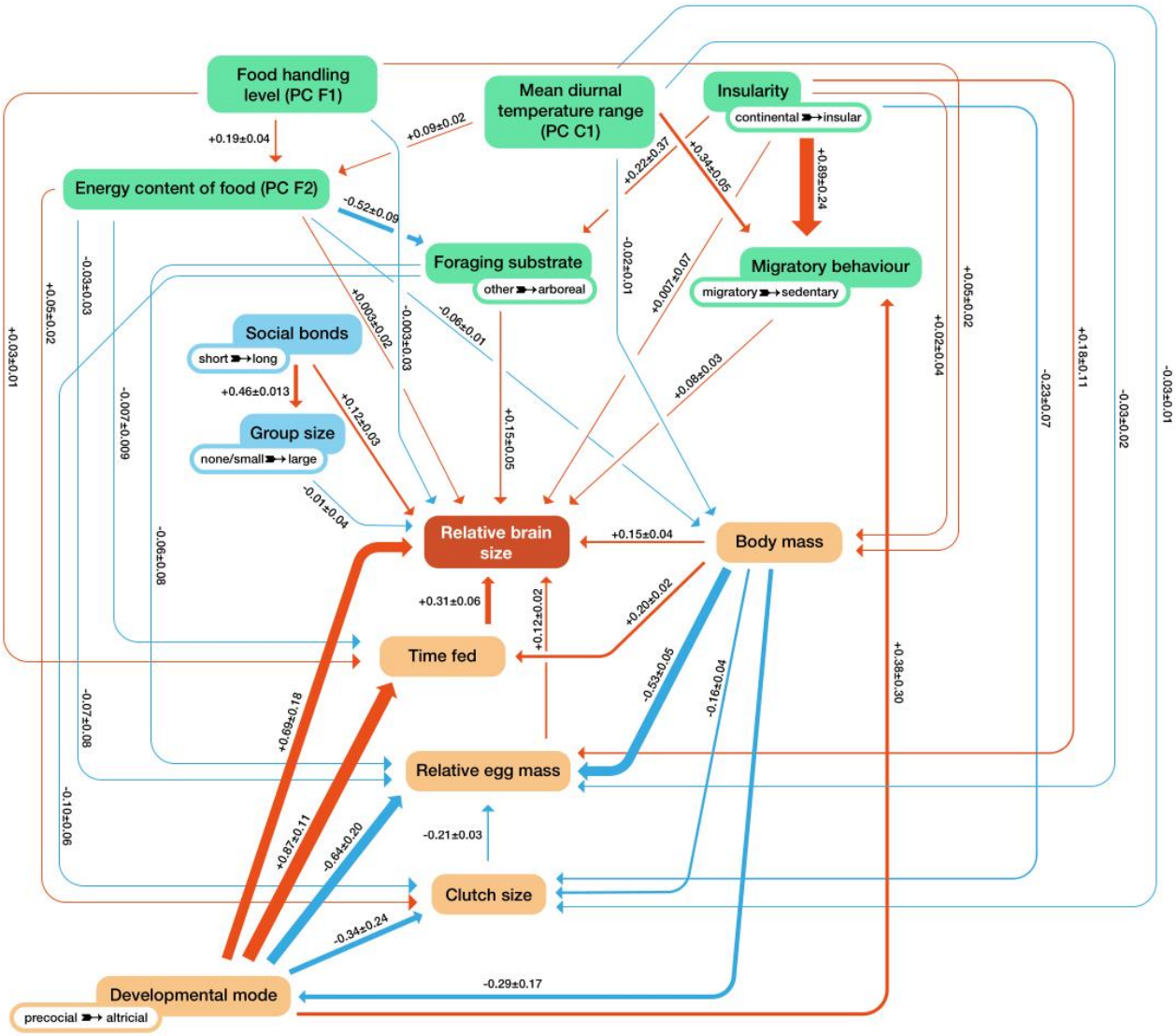
Competing interests

None.

Materials & Correspondence

M.G.

642 **Supporting Information**



S1 Fig. Phylogenetic associations among parental provisioning (orange), ecological and social
645 **predictors (green) and relative brain size, assessed by d-separation path analyses** (34) **(N=1,176 bird species).** Arrow thickness and numeric values show the strength of the association, arrow color its direction (orange: positive, blue: negative).

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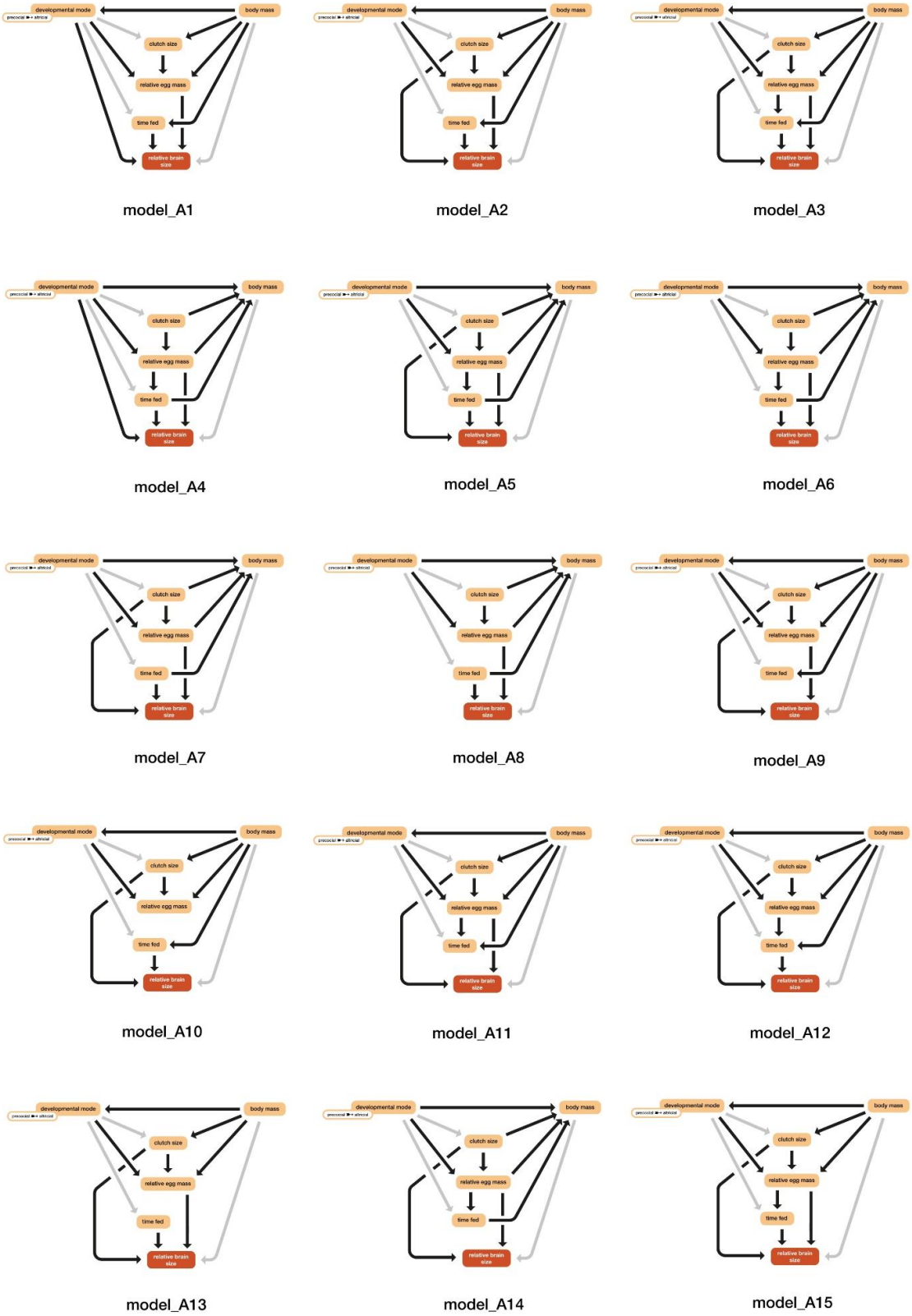
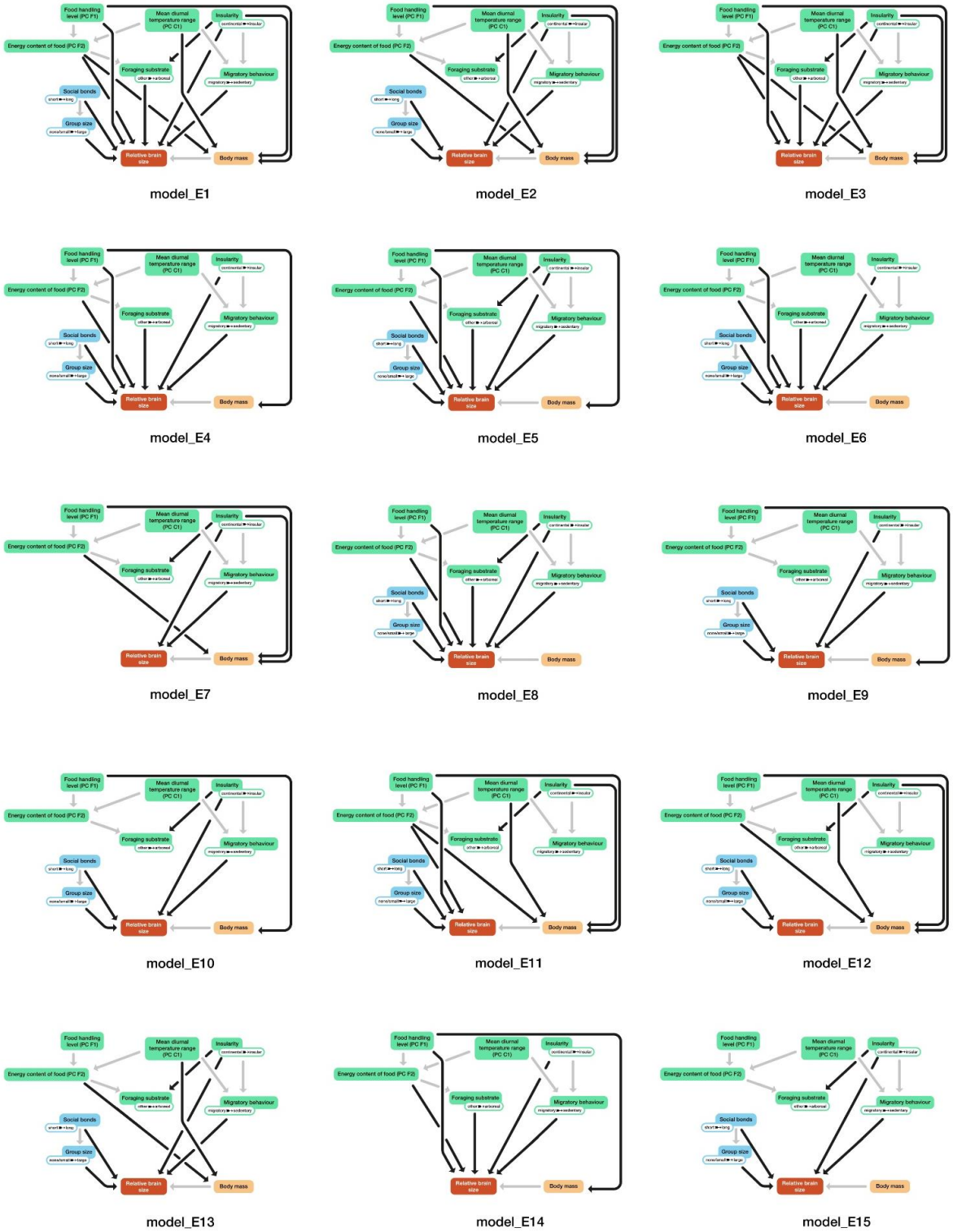
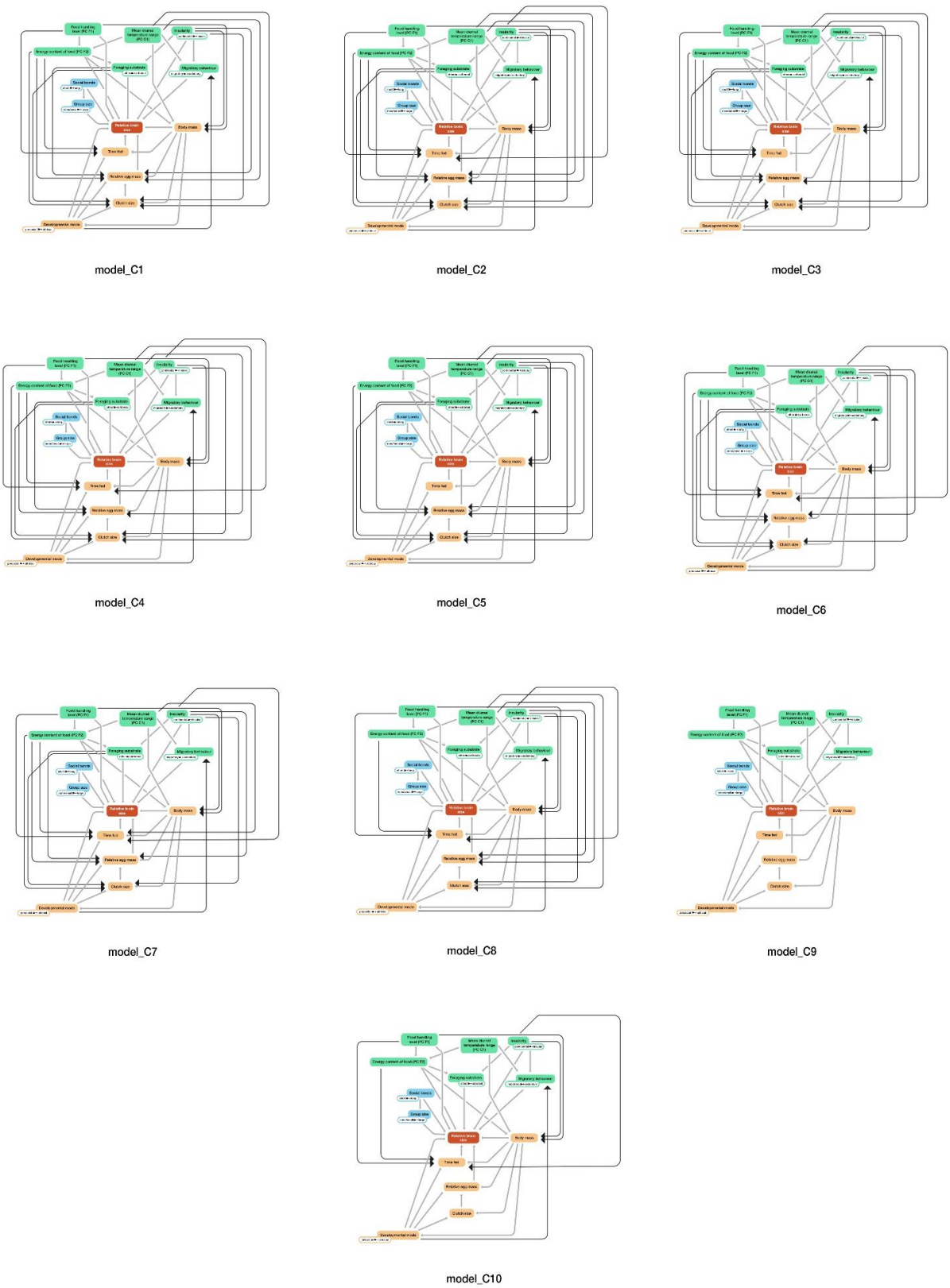


S2 Fig. Network topologies of the top 15 parental provisioning models of the phylogenetic path analyses, arranged by increasing cCIC. Grey arrows indicate relationships retained in all models, black arrows indicate relationships that varied between different models.



S3 Fig. Network topologies of the top 15 eco-social models of the phylogenetic path analyses, arranged by increasing cCIC. Grey arrows indicate relationships retained in all models, black arrows indicate relationships that varied between different models.



S4 Fig. Network topologies of all 10 combined models of the phylogenetic path analyses, arranged by increasing cCIC. Grey arrows indicate relationships retained in all models, black arrows indicate relationships that varied between different models.

S1a-c Table. Phylogenetically controlled mixed models in MCMCglmm(33) assessing the effect on *absolute* brain size in birds (N=1,176 species) of a) parental provisioning predictors, b) eco-social predictors, and c) both combined.

	Predictor	Post. mean	lower ▪ upper 95% CI	N	p MCMC
a) Parental investment model	**Intercept**	**-0.30**	**-0.46 ▪ -0.11**	**1000**	**<0.001**
	Mass	-0.03	-0.07 ▪ 0.01	893	0.11
	Development mode (precocial vs altricial)	0.12	-0.02 ▪ 0.25	1000	0.10
	Clutch size	**-0.07**	**-0.09 ▪ -0.04**	**1000**	**<0.001**
	Residual egg mass	**0.09**	**0.04 ▪ 0.14**	**1000**	**0.002**
	Time fed	**0.09**	**0.04 ▪ 0.14**	**1000**	**<0.001**
	Number of caretakers	0.00	-0.01 ▪ 0.01	1000	0.51
	Mass x development mode	**0.18**	**0.13 ▪ 0.24**	**1000**	**<0.001**
	Mass x clutch size	**0.02**	**0.01 ▪ 0.04**	**1000**	**0.008**
	Mass x residual egg mass	**0.07**	**0.03 ▪ 0.11**	**1000**	**<0.001**
	Development mode x clutch size	**0.09**	**0.06 ▪ 0.13**	**1000**	**<0.001**
	Development mode x residual egg mass	**0.19**	**0.12 ▪ 0.28**	**1087**	**<0.001**
	Development mode x time fed	0.07	0.00 ▪ 0.16	1000	0.051
	Residual egg mass x clutch size	**0.09**	**0.07 ▪ 0.11**	**1000**	**<0.001**
b) Eco-social model	**Intercept**	**-0.4**	**-0.57 ▪ -0.22**	**1155**	**<0.001**
	Mass	**0.98**	**0.95 ▪ 1**	**1000**	**<0.001**
	Foraging substrate (others vs arboreal)	**0.11**	**0.06 ▪ 0.15**	**954**	**<0.001**
	Migratory behavior (sedentary vs migratory)	**0.05**	**0.03 ▪ 0.07**	**1190**	**<0.001**
	Energy content of food (PC)	0.00	-0.01 ▪ 0.01	1000	0.92
	Food handling level (PC)	0.00	-0.02 ▪ 0.02	1000	0.93
	Insularity (continental vs insular)	0.00	-0.04 ▪ 0.06	1000	0.89
	Mean diurnal temperature range (PC)	0.00	0.00 ▪ 0.01	1000	0.33
	Annual temperature and rainfall (PC)	-0.01	-0.03 ▪ 0.00	1000	0.064
	Climatic seasonality (PC)	0.00	-0.01 ▪ 0.01	1000	0.88
	Short vs seasonal social bonds	0.03	-0.01 ▪ 0.09	1000	0.18
	Short vs long-term social bonds	**0.07**	**0.02 ▪ 0.13**	**1000**	**0.002**
	Colonial vs solitary breeding	0.00	-0.02 ▪ 0.02	1131	0.82
	Asocial vs pair living	-0.03	-0.06 ▪ 0.01	1000	0.11
	Asocial vs small groups	-0.02	-0.05 ▪ 0.02	1000	0.35
	Asocial vs large groups	0.00	-0.03 ▪ 0.03	1288	0.96
	Mass x foraging substrate	**0.1**	**0.06 ▪ 0.14**	**861**	**<0.001**
	Mass x sedentariness	**-0.03**	**-0.05 ▪ -0.01**	**1000**	**0.01**
	Mass x energy content of food (PC)	**0.02**	**0.01 ▪ 0.03**	**1000**	**0.004**
c) Combined model	**Intercept**	**-0.36**	**-0.55 ▪ -0.18**	**1000**	**<0.001**
	Mass	**0.94**	**0.90 ▪ 0.97**	**901**	**<0.001**
	Development mode (precocial vs altricial)	**0.17**	**0.05 ▪ 0.29**	**1000**	**0.01**
	Clutch size	**-0.06**	**-0.09 ▪ -0.04**	**1000**	**<0.001**
	Residual egg mass	**0.1**	**0.05 ▪ 0.14**	**1000**	**<0.001**
	Time fed	**0.06**	**0.01 ▪ 0.11**	**1000**	**0.018**
	Number of caretakers	0.00	-0.01 ▪ 0.01	1000	0.67
	Mass x development mode	**0.16**	**0.11 ▪ 0.21**	**891**	**<0.001**
	Mass x clutch size	**0.02**	**0.00 ▪ 0.03**	**1000**	**0.016**
	Mass x residual egg mass	**0.06**	**0.03 ▪ 0.09**	**1000**	**<0.001**
	Development mode x clutch size	**0.11**	**0.08 ▪ 0.15**	**1000**	**<0.001**
	Development mode x residual egg mass	**0.17**	**0.10 ▪ 0.24**	**1000**	**<0.001**
	Development mode x time fed	0.07	0.00 ▪ 0.15	1000	0.078
	Residual egg mass x clutch size	**0.08**	**0.06 ▪ 0.10**	**1108**	**<0.001**
	Foraging substrate (others vs arboreal)	**0.09**	**0.05 ▪ 0.14**	**1000**	**<0.001**
	Migratory behavior (sedentary vs migratory)	**0.04**	**0.02 ▪ 0.06**	**1079**	**<0.001**
	Energy content of food (PC)	0.01	0.00 ▪ 0.03	1179	0.056
	Food handling level (PC)	0.02	-0.01 ▪ 0.04	972	0.22
	Insularity (continental vs insular)	0.01	-0.03 ▪ 0.06	1000	0.68
	Mean diurnal temperature range (PC)	0.00	-0.01 ▪ 0.01	1000	0.64
	Annual temperature and rainfall (PC)	-0.01	-0.02 ▪ 0.00	1000	0.23
	Climatic seasonality (PC)	0.00	-0.01 ▪ 0.01	1000	0.53
	Short vs seasonal social bonds	-0.01	-0.06 ▪ 0.04	1000	0.77
	Short vs long-term social bonds	0.02	-0.03 ▪ 0.07	1000	0.39
	Colonial vs solitary breeding	-0.01	-0.03 ▪ 0.02	1000	0.59
	Asocial vs pair living	-0.03	-0.06 ▪ 0.00	1098	0.10
	Asocial vs small groups	-0.02	-0.05 ▪ 0.01	1000	0.27
	Asocial vs large groups	0.00	-0.03 ▪ 0.02	1215	0.78
	Mass x foraging substrate	**0.06**	**0.02 ▪ 0.10**	**1000**	**0.008**
	Mass x sedentariness	**-0.03**	**-0.05 ▪ -0.01**	**1000**	**<0.001**
	Mass x energy content of food (PC)	0.01	0.00 ▪ 0.02	1000	0.13

Developmental mode x food handling level (PC)	**-0.05**	**-0.08 ▪ -0.01**	**900**	**0.018**
Clutch size x energy content of food (PC)	**-0.01**	**-0.02 ▪ 0.00**	**1000**	**0.04**
Clutch size x food handling level (PC)	**-0.01**	**-0.03 ▪ 0.00**	**1000**	**0.014**

Significant predictors are highlighted in bold. Post. mean = mean of the posterior distribution of a parameter, CI = posterior credibility interval, N = effective sample size (corrected for MCMC timeseries autocorrelation), p MCMC = P-value. The Principal Component analyses (PCAs) of climatic and food parameters are shown in S4 Table.

S2a-d Table. Phylogenetically controlled mixed models in MCMCglmm(33) assessing the effect on *relative* brain size in birds (model a-c: N=1,176 species, model d: N= 886 species) of a) parental provisioning predictors, b) eco-social predictors, c) both combined, and d) both combined and including longevity.

	Predictor	Post. mean	lower ▪ upper 95% CI	p MCMC
a) Parental investment model	**Intercept**	**-0.29**	**-0.49 ▪ -0.10**	**1**
	Mass	-0.03	-0.07 ▪ 0.01	0.02
	Development mode (precocial vs altricial)	0.11	-0.02 ▪ 0.24	0.04
	Clutch size	**-0.07**	**-0.10 ▪ -0.04**	**1**
	Residual egg mass	**0.10**	**0.04 ▪ 0.15**	**1**
	Time fed	**0.09**	**0.04 ▪ 0.14**	**1**
	Number of caretakers	0.00	-0.01 ▪ 0.01	0
	Mass x development mode	**0.19**	**0.13 ▪ 0.24**	**1**
	Mass x clutch size	**0.02**	**0.01 ▪ 0.04**	**1**
	Mass x residual egg mass	**0.07**	**0.03 ▪ 0.10**	**1**
	Development mode x clutch size	**0.09**	**0.05 ▪ 0.13**	**1**
	Development mode x residual egg mass	**0.19**	**0.11 ▪ 0.27**	**1**
	Development mode x time fed	0.07	-0.01 ▪ 0.15	0
	Residual egg mass x clutch size	**0.09**	**0.06 ▪ 0.11**	**1**
b) Eco-social model	**Intercept**	**-0.44**	**-0.64 ▪ -0.24**	**1**
	Mass	**0.05**	**0.02 ▪ 0.07**	**1**
	Foraging substrate (others vs arboreal)	**0.12**	**0.07 ▪ 0.17**	**1**
	Migratory behavior (sedentary vs migratory)	**0.05**	**0.02 ▪ 0.07**	**1**
	Energy content of food (PC)	0.00	-0.01 ▪ 0.01	0
	Food handling level (PC)	0.00	-0.02 ▪ 0.02	0
	Insularity (continental vs insular)	0.00	-0.05 ▪ 0.06	0
	Mean diurnal temperature range (PC)	0.01	0.00 ▪ 0.02	0
	Annual temperature and rainfall (PC)	-0.01	-0.03 ▪ 0.00	0.34
	Climatic seasonality (PC)	0.00	-0.01 ▪ 0.01	0
	Short vs seasonal social bonds	0.04	-0.02 ▪ 0.09	0
	Short vs long-term social bonds	**0.08**	**0.02 ▪ 0.14**	**1**
	Colonial vs solitary breeding	0.00	-0.02 ▪ 0.03	0
	Asocial vs pair living	-0.03	-0.06 ▪ 0.01	0
	Asocial vs small groups	-0.02	-0.06 ▪ 0.02	0
	Asocial vs large groups	0.00	-0.04 ▪ 0.03	0
	Mass x foraging substrate	**0.10**	**0.06 ▪ 0.15**	**1**
	Mass x sedentariness	**-0.03**	**-0.05 ▪ -0.01**	**1**
	Mass x energy content of food (PC)	**0.02**	**0.01 ▪ 0.03**	**1**
c) Combined model	**Intercept**	**-0.37**	**-0.57 ▪ -0.17**	**1**
	Mass	-0.01	-0.05 ▪ 0.03	0
	Development mode (precocial vs altricial)	**0.17**	**0.04 ▪ 0.30**	**0.99**
	Clutch size	**-0.07**	**-0.10 ▪ -0.04**	**1**
	Residual egg mass	**0.10**	**0.05 ▪ 0.16**	**1**
	Time fed	**0.07**	**0.02 ▪ 0.12**	**1**
	Number of caretakers	0.00	-0.01 ▪ 0.01	0
	Mass x development mode	**0.18**	**0.13 ▪ 0.23**	**1**
	Mass x clutch size	**0.02**	**0.00 ▪ 0.04**	**1**
	Mass x residual egg mass	**0.07**	**0.03 ▪ 0.10**	**1**
	Development mode x clutch size	**0.12**	**0.08 ▪ 0.16**	**1**
	Development mode x residual egg mass	**0.19**	**0.11 ▪ 0.27**	**1**
	Development mode x time fed	0.07	-0.01 ▪ 0.15	0.02
	Residual egg mass x clutch size	**0.09**	**0.07 ▪ 0.11**	**1**
	Foraging substrate (others vs arboreal)	**0.10**	**0.05 ▪ 0.14**	**1**
	Migratory behavior (sedentary vs migratory)	**0.05**	**0.02 ▪ 0.07**	**1**
	Energy content of food (PC)	0.01	0.00 ▪ 0.03	0.05
	Food handling level (PC)	0.02	-0.01 ▪ 0.05	0
	Insularity (continental vs insular)	0.01	-0.04 ▪ 0.05	0
	Mean diurnal temperature range (PC)	0.00	-0.01 ▪ 0.01	0
	Annual temperature and rainfall (PC)	-0.01	-0.02 ▪ 0.00	0
	Climatic seasonality (PC)	0.00	0.00 ▪ 0.01	0
	Short vs seasonal social bonds	-0.01	-0.06 ▪ 0.04	0
	Short vs long-term social bonds	0.02	-0.03 ▪ 0.08	0
	Colonial vs solitary breeding	-0.01	-0.03 ▪ 0.02	0
	Asocial vs pair living	-0.03	-0.06 ▪ 0.01	0.01
	Asocial vs small groups	-0.02	-0.06 ▪ 0.02	0
	Asocial vs large groups	-0.01	-0.04 ▪ 0.03	0
	Mass x foraging substrate	**0.06**	**0.02 ▪ 0.10**	**1**

	Mass x sedentariness	**-0.03**	**-0.05 ▪ -0.01**	**1**
	Developmental mode x food handling level (PC)	**-0.05**	**-0.09 ▪ -0.02**	**1**
	Clutch size x energy content of food (PC)	-0.01	-0.02 ▪ 0.00	0.36
	Clutch size x food handling level (PC)	**-0.01**	**-0.03 ▪ 0.00**	**0.96**
d) Combined model including longevity	**Intercept**	**-0.36**	**-0.58 ▪ -0.14**	**1**
	Mass	0.01	-0.04 ▪ 0.06	0
	Development mode (precocial vs altricial)	**0.18**	**0.04 ▪ 0.33**	**0.99**
	Clutch size	**-0.08**	**-0.12 ▪ -0.04**	**1**
	Residual egg mass	**0.12**	**0.05 ▪ 0.18**	**1**
	Time fed	0.05	0.00 ▪ 0.11	0.1
	Number of caretakers	0.00	-0.01 ▪ 0.01	0
	Mass x development mode	**0.15**	**0.09 ▪ 0.22**	**1**
	Mass x clutch size	0.01	-0.01 ▪ 0.03	0
	Mass x residual egg mass	0.04	0.00 ▪ 0.08	0.26
	Development mode x clutch size	**0.13**	**0.09 ▪ 0.18**	**1**
	Development mode x residual egg mass	**0.17**	**0.08 ▪ 0.26**	**1**
	Development mode x time fed	**0.13**	**0.04 ▪ 0.23**	**1**
	Residual egg mass x clutch size	**0.08**	**0.06 ▪ 0.11**	**1**
	Foraging substrate (others vs arboreal)	**0.09**	**0.04 ▪ 0.14**	**1**
	Migratory behavior (sedentary vs migratory)	**0.04**	**0.01 ▪ 0.07**	**1**
	Energy content of food (PC)	0.01	0.00 ▪ 0.03	0
	Food handling level (PC)	0.01	-0.03 ▪ 0.04	0
	Insularity (continental vs insular)	-0.01	-0.07 ▪ 0.05	0
	Mean diurnal temperature range (PC)	-0.01	-0.02 ▪ 0.01	0
	Annual temperature and rainfall (PC)	0.00	-0.02 ▪ 0.01	0
	Climatic seasonality (PC)	0.00	-0.01 ▪ 0.01	0
	Short vs seasonal social bonds	0.00	-0.07 ▪ 0.06	0
	Short vs long-term social bonds	0.04	-0.03 ▪ 0.11	0
	Colonial vs solitary breeding	-0.01	-0.04 ▪ 0.01	0
	Asocial vs pair living	-0.02	-0.06 ▪ 0.02	0
	Asocial vs small groups	-0.04	-0.08 ▪ 0.01	0
	Asocial vs large groups	0.00	-0.04 ▪ 0.04	0
	Mass x foraging substrate	**0.06**	**0.01 ▪ 0.11**	**0.98**
	Mass x sedentariness	**-0.03**	**-0.05 ▪ -0.01**	**1**
	Mass x energy content of food (PC)	0.01	-0.01 ▪ 0.02	0
	Developmental mode x food handling level (PC)	-0.05	-0.09 ▪ 0.00	0.71
	Clutch size x energy content of food (PC)	-0.01	-0.03 ▪ 0.00	0.12
	Clutch size x food handling level (PC)	-0.01	-0.03 ▪ 0.00	0.02
	Longevity	0.01	-0.01 ▪ 0.02	0
	Mass x longevity	**-0.01**	**-0.03 ▪ 0.00**	**0.98**

Significant predictors that are supported by at least 95% of different models are highlighted in bold. Post. mean = mean of the posterior distribution of a parameter, CI = posterior credibility interval, p MCMC = averaged P-values over all 200 models with different phylogenetic trees. The Principal Component analyses (PCAs) of climatic and food parameters are shown in S4 Table.

S3 Table. Additional phylogenetically controlled mixed models in MCMCglmm(33) assessing the effect of parental provisioning and eco-social parameters on the evolution of relative brain size in birds.

	Predictor	Post. mean	lower ▪ upper 95% CI	N	pMCMC
a) excluding duration parental provisioning	**Intercept**	**-0.44**	**-0.64 ▪ -0.26**	**1000**	**<0.001**
	Mass	-0.01	-0.04 ▪ 0.03	1000	0.77
	Development mode (precocial vs altricial)	**0.24**	**0.13 ▪ 0.36**	**977**	**<0.001**
	Clutch size	**-0.07**	**-0.10 ▪ -0.04**	**1722**	**<0.001**
	Residual egg mass	**0.05**	**0.00 ▪ 0.10**	**895**	**0.034**
	Number of caretakers	0.00	-0.01 ▪ 0.01	1000	0.42
	Mass x development mode	**0.19**	**0.14 ▪ 0.24**	**1000**	**<0.001**
	Mass x clutch size	**0.02**	**0.01 ▪ 0.03**	**1000**	**<0.001**
	Mass x residual egg mass	**0.11**	**0.08 ▪ 0.14**	**1117**	**<0.001**
	Development mode x clutch size	**0.11**	**0.07 ▪ 0.15**	**1446**	**<0.001**
	Development mode x residual egg mass	**0.27**	**0.21 ▪ 0.34**	**1000**	**<0.001**
	Residual egg mass x clutch size	**0.08**	**0.06 ▪ 0.10**	**1000**	**<0.001**
	Foraging substrate (others vs arboreal)	**0.11**	**0.08 ▪ 0.15**	**1000**	**<0.001**
	Migratory behavior (sedentary vs migratory)	**0.05**	**0.03 ▪ 0.07**	**980**	**<0.001**
	Energy content of food (PC)	**0.02**	**0.00 ▪ 0.03**	**1000**	**0.008**
	Food handling level (PC)	0.02	-0.01 ▪ 0.04	1151	0.16
	Insularity (continental vs insular)	0.03	-0.01 ▪ 0.08	1000	0.13
	Mean diurnal temperature range (PC)	0.00	-0.01 ▪ 0.01	1220	1.00
	Annual temperature and rainfall (PC)	**-0.01**	**-0.02 ▪ 0.00**	**1000**	**0.018**
	Climatic seasonality (PC)	0.00	-0.01 ▪ 0.01	1000	0.90
	Short vs seasonal social bonds	-0.02	-0.07 ▪ 0.03	844	0.48
	Short vs long-term social bonds	0.01	-0.04 ▪ 0.06	876	0.77
	Colonial vs solitary breeding	0.00	-0.02 ▪ 0.02	1000	0.73
	Asocial vs pair living	-0.01	-0.05 ▪ 0.01	978	0.36
	Asocial vs small groups	-0.01	-0.05 ▪ 0.02	1000	0.61
	Asocial vs large groups	0.01	-0.02 ▪ 0.04	1000	0.38
	Mass x foraging substrate	**0.07**	**0.03 ▪ 0.11**	**1000**	**0.002**
	Mass x sedentariness	**-0.03**	**-0.05 ▪ -0.01**	**1000**	**<0.001**
	Developmental mode x food handling level (PC)	**-0.04**	**-0.08 ▪ -0.01**	**1115**	**0.016**
	Clutch size x energy content of food (PC)	**-0.01**	**-0.02 ▪ 0.00**	**1000**	**0.044**
	Clutch size x food handling level (PC)	**-0.01**	**-0.02 ▪ 0.00**	**1189**	**0.02**
b) excluding parental provisioning and social grouping	**Intercept**	**-0.45**	**-0.62 ▪ -0.27**	**1000**	**<0.001**
	Mass	0.00	-0.04 ▪ 0.04	1099	0.99
	Development mode (precocial vs altricial)	**0.23**	**0.12 ▪ 0.34**	**1000**	**<0.001**
	Clutch size	**-0.06**	**-0.09 ▪ -0.04**	**1000**	**<0.001**
	Residual egg mass	**0.08**	**0.03 ▪ 0.13**	**1000**	**0.006**
	Number of caretakers	0.01	0.00 ▪ 0.01	1020	0.18
	Mass x development mode	**0.16**	**0.11 ▪ 0.21**	**1000**	**<0.001**
	Mass x clutch size	**0.02**	**0.00 ▪ 0.03**	**1108**	**0.008**
	Mass x residual egg mass	**0.09**	**0.06 ▪ 0.12**	**1097**	**<0.001**
	Development mode x clutch size	**0.09**	**0.05 ▪ 0.12**	**1000**	**<0.001**
	Development mode x residual egg mass	**0.19**	**0.14 ▪ 0.26**	**1000**	**<0.001**
	Residual egg mass x clutch size	**0.08**	**0.06 ▪ 0.10**	**1000**	**<0.001**
	Foraging substrate (others vs arboreal)	**0.11**	**0.08 ▪ 0.15**	**1000**	**<0.001**
	Migratory behavior (sedentary vs migratory)	**0.06**	**0.04 ▪ 0.07**	**1000**	**<0.001**
	Energy content of food (PC)	0.01	0.00 ▪ 0.02	1093	0.062
	Food handling level (PC)	0.01	-0.01 ▪ 0.04	1000	0.34
	Insularity (continental vs insular)	0.02	-0.03 ▪ 0.06	1000	0.41
	Mean diurnal temperature range (PC)	0.00	-0.01 ▪ 0.01	1000	0.60
	Annual temperature and rainfall (PC)	**-0.01**	**-0.02 ▪ 0.00**	**1359**	**0.046**
	Climatic seasonality (PC)	0.00	-0.01 ▪ 0.01	1506	0.79
	Short vs seasonal social bonds	-0.02	-0.07 ▪ 0.03	1100	0.48
	Short vs long-term social bonds	0.01	-0.04 ▪ 0.06	1000	0.79
	Colonial vs solitary breeding	-0.01	-0.03 ▪ 0.02	1000	0.61
	Mass x foraging substrate	**0.07**	**0.04 ▪ 0.11**	**1000**	**<0.001**
	Mass x sedentariness	**-0.03**	**-0.05 ▪ -0.01**	**1000**	**0.002**
	Developmental mode x food handling level (PC)	-0.03	-0.06 ▪ 0.00	1000	0.052
	Clutch size x food handling level (PC)	**-0.01**	**-0.02 ▪ 0.00**	**1000**	**0.008**
c) using 4 developmental mode categories	Intercept	-0.11	-0.32 ▪ 0.06	1000	0.25
	Mass	**0.17**	**0.14 ▪ 0.21**	**1134**	**<0.001**
	Development mode (altricial vs precocial)	-0.23	-0.53 ▪ 0.11	1000	0.16
	Development mode (altricial vs semi-altricial)	-0.13	-0.32 ▪ 0.05	985	0.17
	Development mode (altricial vs semi-precocial)	**-0.26**	**-0.41 ▪ -0.11**	**1000**	**<0.001**
	Clutch size	0.02	-0.01 ▪ 0.05	1000	0.11

Residual egg mass	**0.29**	**0.22 ▪ 0.36**	**1000**	**<0.001**
Time fed	**0.20**	**0.13 ▪ 0.27**	**874**	**<0.001**
Number of caretakers	0.00	-0.01 ▪ 0.01	1000	0.71
Mass x development mode (altricial vs precocial)	**-0.22**	**-0.28 ▪ -0.16**	**1120**	**<0.001**
Mass x development mode (altricial vs semi-altricial)	-0.03	-0.12 ▪ 0.07	1000	0.54
Mass x development mode (alt. vs semi-precocial)	**-0.13**	**-0.21 ▪ -0.06**	**1000**	**<0.001**
Mass x clutch size	0.02	0.00 ▪ 0.04	1000	0.05
Mass x residual egg mass	**0.06**	**0.02 ▪ 0.10**	**1000**	**0.002**
Development mode (alt. vs precocial) x clutch size	**-0.06**	**-0.11 ▪ -0.01**	**1000**	**0.012**
Development mode (alt. vs semi-altricial) x clutch size	-0.01	-0.07 ▪ 0.07	1000	**0.89**
Development mode (alt. vs semi-prec.) x clutch size	**-0.13**	**-0.19 ▪ -0.07**	**1000**	**<0.001**
Develop. mode (alt. vs prec.) x residual egg mass	**-0.19**	**-0.33 ▪ -0.08**	**1095**	**0.002**
Develop. mode (alt. vs semi-alt.) x residual egg mass	0.06	-0.14 ▪ 0.25	1000	**0.484**
Develop. mode (alt. vs semi-prec.) x res. egg mass	**-0.19**	**-0.29 ▪ -0.08**	**1095**	**<0.001**
Development mode (altricial vs precocial) x time fed	-0.12	-0.30 ▪ 0.06	1000	**0.164**
Development mode (alt. vs semi-altricial) x time fed	**-0.14**	**-0.3 ▪ -0.01**	**764**	**0.048**
Development mode (alt. vs semi-prec.) x time fed	**-0.18**	**-0.27 ▪ -0.07**	**1000**	**<0.001**
Residual egg mass x clutch size	**0.09**	**0.05 ▪ 0.12**	**1000**	**<0.001**

Model **a)** combined model excluding the duration of parental provisioning: N = 1,458 species; model **b)** combined model excluding parental provisioning and social grouping parameters: N = 1,594 species; model **c)** using four developmental mode categories: N=1,176 species. Significant predictors are highlighted in bold. Post. mean = mean of the posterior distribution of a parameter, CI = posterior credibility interval, N = effective sample size (corrected for MCMC timeseries autocorrelation). The Principal Component analyses (PCAs) of climatic and food parameters are shown in S4 Table.

S4 Table. Principal Component Analyses (PCA) loadings and variance explained. Loadings of the main contributors to the different component are highlighted in bold.

a) Food PCA	PC F1	PC F2
Food energy content / 100g	0.12	**0.99**
Food fiber content / 100g	**-0.96**	-0.04
Food handling levels	**0.95**	0.17
SS loadings	1.84	1.01
Proportion Variance	0.61	0.34
Cumulative Variance	0.61	0.95
Proportion Explained	0.64	0.36
Cumulative Proportion	0.64	1.00

b) Climatic PCA	PC C1	PC C2	PC C3
Bio1_mean Annual Mean Temperature	**0.89**	0.06	0.04
Bio1_stdev	**-0.62**	**0.53**	0.04
Bio2_mean Mean Diurnal Range	-0.14	0.19	**0.81**
Bio2_stdev	-0.30	**0.71**	0.43
Bio3_mean Isothermality	**0.89**	-0.02	-0.22
Bio3_stdev	-0.02	0.87	0.10
Bio4_mean Temperature Seasonality	**-0.96**	0.02	0.13
Bio4_stdev	**-0.78**	0.50	0.14
Bio7_mean Temperature Annual Range	**-0.90**	0.08	0.34
Bio7_stdev	**-0.69**	**0.61**	0.22
Bio12_mean Annual Precipitation	**0.56**	-0.01	**-0.73**
Bio12_stdev	0.28	0.65	-0.44
Bio15_mean Precipitation Seasonality	0.01	0.17	**0.80**
Bio15_stdev	-0.11	0.74	0.39
SS loadings	5.32	3.22	2.63
Proportion Variance	0.38	0.23	0.19
Cumulative Variance	0.38	0.61	0.80
Proportion Explained	0.48	0.29	0.24
Cumulative Proportion	0.48	0.76	1.00

a) Food items PCA. **b)** Climatic PCA.

S5 Table. Variance inflation factor (VIF) analyses of all parameters included in the combined model.

Predictor	VIF
Mass	1.188
Development mode (precocial vs altricial)	1.162
Clutch size	1.219
Residual egg mass	1.273
Time fed	1.906
Number of caretakers	1.167
Foraging substrate (others vs arboreal)	1.075
Migratory behavior (sedentary vs migratory)	1.352
Energy content of food (PC)	1.095
Food handling level (PC)	1.135
Insularity (continental vs insular)	1.564
Mean diurnal temperature range (PC)	1.600
Annual temperature and rainfall (PC)	2.076
Climatic seasonality (PC)	1.108
Social bonds	1.567
Colonial vs solitary breeding	1.031
Grouping pattern	1.073

Variance inflation factors (VIF) were calculated from a Bayesian phylogenetically controlled mixed model including parental provisioning and eco-social predictors. VIF is assumed to be the term inflating the regression coefficient's variance estimate $\widehat{var}(\beta_i) = \left(\frac{s^2}{(n-1)\widehat{var}(X_i)}\right)\frac{1}{1-R_i^2} = \left(\frac{s^2}{(n-1)\widehat{var}(X_i)}\right)VIF_i$, where s^2 is the root mean squared error of regression, n is the sample size, X_i is the i-th column of the design matrix. R_i^2 then becomes the GLMM R^2 analogue for the model: $X_i = \alpha_0 + \alpha_1 X_1 + \cdots + \alpha_{i-1}X_{i-1} + \alpha_{i+1}X_{i+1} + \cdots + \alpha_k X_k$.

S6 Table. Model comparisons of the models included in the phylogenetic d-separation path analyses.

	Model	C	CICc	ΔCICc
a, Parental provisioning model	Model_A1	54.22	92.88	0.00
	Model_A2	62.77	99.36	6.48
	Model_A3	62.07	100.72	7.85
	Model_A4	72.04	110.70	17.82
	Model_A5	79.89	118.54	25.67
	Model_A6	87.46	124.05	31.17
	Model_A7	91.65	128.24	35.36
	Model_A8	99.22	133.75	40.87
	Model_A9	116.06	150.59	57.71
	Model_A10	119.17	151.64	58.77
	Model_A11	115.36	151.95	59.07
	Model_A12	118.47	153.00	60.12
	Model_A13	134.86	169.39	76.51
	Model_A14	133.18	169.77	76.89
	Model_A15	134.15	170.74	77.87
	Model_A16	136.29	170.82	77.94
	Model_A17	141.97	174.44	81.56
	Model_A18	141.26	175.79	82.92
	Model_A19	141.72	176.25	83.37
	Model_A20	144.94	179.47	86.59
	Model_A21	148.05	180.52	87.64
	Model_A22	152.56	185.03	92.15
	Model_A23	151.97	188.57	95.69
	Model_A24	154.53	189.06	96.18
	Model_A25	160.02	192.49	99.62
	Model_A26	159.09	193.61	100.74
	Model_A27	159.54	194.07	101.20
	Model_A28	160.00	194.53	101.65
	Model_A29	163.73	198.26	105.39
	Model_A30	170.85	203.32	110.44
	Model_A31	171.30	203.77	110.90
	Model_A32	172.36	206.88	114.01
	Model_A33	177.82	212.35	119.48
	Model_A34	181.43	213.90	121.03
	Model_A35	187.43	217.84	124.96
	Model_A36	187.41	219.87	127.00
	Model_A37	187.41	219.87	127.00
	Model_A38	188.15	220.62	127.74
	Model_A39	188.90	221.37	128.49
	Model_A40	191.26	221.67	128.80
	Model_A41	187.44	221.97	129.09
	Model_A42	190.56	223.02	130.15
	Model_A43	205.23	237.70	144.82
	Model_A44	205.23	237.70	144.82
	Model_A45	205.26	239.79	146.92
	Model_A46	208.38	240.85	147.97

	Model	C	CICc	ΔCICc
b, Eco-social model	Model_E1	222.73	282.24	0.00
	Model_E2	238.15	291.37	9.13
	Model_E3	241.22	296.54	14.29
	Model_E4	242.74	298.06	15.82
	Model_E5	242.16	299.57	17.33
	Model_E6	249.66	302.88	20.63
	Model_E7	254.88	303.92	21.67
	Model_E8	249.07	304.39	22.14
	Model_E9	258.17	307.21	24.96
	Model_E10	257.58	308.71	26.46
	Model_E11	255.57	308.79	26.54
	Model_E12	260.31	309.35	27.10
	Model_E13	265.08	312.04	29.79
	Model_E14	261.24	312.37	30.12
	Model_E15	264.49	313.54	31.29
	Model_E16	260.65	313.87	31.62
	Model_E17	268.15	317.19	34.95
	Model_E18	267.56	318.69	36.45
	Model_E19	274.89	319.77	37.53
	Model_E20	274.31	321.26	39.02
	Model_E21	272.62	323.75	41.50
	Model_E22	281.81	324.61	42.36
	Model_E23	275.81	324.85	42.60
	Model_E24	280.54	325.42	43.18
	Model_E25	281.22	326.10	43.85
	Model_E26	275.00	326.13	43.88
	Model_E27	279.73	326.69	44.45
	Model_E28	282.72	329.68	47.43
	Model_E29	287.46	330.26	48.01
	Model_E30	281.91	330.95	48.71
	Model_E31	286.65	331.53	49.28
	Model_E32	292.64	339.59	57.35
	Model_E33	292.05	341.09	58.84
	Model_E34	299.55	344.43	62.18
	Model_E35	298.96	345.92	63.67
	Model_E36	308.51	351.31	69.06
	Model_E37	316.24	354.90	72.65
c, Combined model	Model_C1	422.63	544.76	0.00
	Model_C2	420.92	545.26	0.50
	Model_C3	430.92	548.62	3.87
	Model_C4	429.21	549.12	4.36
	Model_C5	429.68	549.59	4.83
	Model_C6	433.82	551.52	6.76
	Model_C7	433.20	553.11	8.35
	Model_C8	444.99	560.49	15.73
	Model_C9	471.68	574.03	29.27
	Model_C10	470.11	576.82	32.06
	Model_C11	933.65	991.06	446.31

720 Models are sorted by their CICc values. Parental provisioning models with a ΔCICc >150 are not shown (N=21 models). C: Fisher's C-statistics. The topologies of the top models (N=15 for parental provisioning and eco-social model, N=10 for combined model) are illustrated in S2-4 Figs.

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